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Population structure of ice-breeding seals

COREY S. DAVIS,* IAN STIRLING,*† CURTIS STROBECK* and DAVID W. COLTMAN*
Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada, †Canadian Wildlife Service, 5320 122 St., Edmonton, AB. T6H 3S5

Abstract

The development of population genetic structure in ice-breeding seal species is likely to be shaped by a combination of breeding habitat and life-history characteristics. Species that return to breed on predictable fast-ice locations are more likely to exhibit natal fidelity than pack-ice-breeding species, which in turn facilitates the development of genetic differentiation between subpopulations. Other aspects of life history such as geographically distinct vocalizations, female gregariousness, and the potential for polygynous breeding may also facilitate population structure. Based on these factors, we predicted that fast-ice-breeding seal species (the Weddell and ringed seal) would show elevated genetic differentiation compared to pack-ice-breeding species (the leopard, Ross, crabeater and bearded seals). We tested this prediction using microsatellite analysis to examine population structure of these six ice-breeding species. Our results did not support this prediction. While none of the Antarctic pack-ice species showed statistically significant population structure, the bearded seal of the Arctic pack ice showed strong differentiation between subpopulations. Again in contrast, the fast-ice-breeding Weddell seal of the Antarctic showed clear evidence for genetic differentiation while the ringed seal, breeding in similar habitat in the Arctic, did not. These results suggest that the development of population structure in ice-breeding phocid seals is a more complex outcome of the interplay of phylogenetic and ecological factors than can be predicted on the basis of breeding substrate and life-history characteristics.

Keywords: Antarctic, Arctic, F_{ST}, microsatellite, pinnipeds, population genetics

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Introduction

Many aspects of the biology and genetics of polar ice-breeding phocids (the 'true seals') are little understood, especially for those species that are widely distributed at low densities in vast remote areas. In such circumstances, even quantifying basic aspects of their biology is challenging. Thus, there is considerably less information about the ecology of ice-breeding phocids in the remote polar regions than of more accessible species where techniques such as direct observation, mark–recapture, or telemetry can be applied (Hoelzel 1997). Molecular techniques are therefore essential for studying population structure of polar ice-breeding species. Multispecies studies using molecular markers can also be used to test hypotheses about how measures of population structure reflect variation in life-history strategies. Here, we investigate whether some aspects of the biology of these species may predict population genetic parameters.

In this study, we examined population structure and genetic diversity of all four Antarctic phocids (Weddell seals, *Leptonychotes weddellii*; crabeater seals, *Lobodon carcinophagus*; leopard seals, *Hydrurga leptonyx*; and Ross seals, *Ommatophoca rossii*) and the two phocid species most adapted to year-round residency in the ice of the circumpolar Arctic (ringed seals, *Phoca hispida* and bearded seals, *Erignathus barbatus*).

In a preliminary study, we demonstrated the ability of microsatellite markers to determine population structure and genetic diversity among three Weddell seal populations, and genetic diversity in one population of leopard seals, and individual crabeater seals from the Amundsen and Bellingshausen seas (Davis *et al*. 2000). In this study, we present a comprehensive description of population structure and genetic diversity in these six polar ice-breeding phocids. We use these results to evaluate the roles that breeding habitat, behaviour and life-history play in predicting population structure.

Correspondence: David W. Coltman, Fax: 780-492-9234; E-mail: dcoltman@ualberta.ca

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Three general habitats are used for parturition and mating by phocid seals (Stirling 1983; Cassini 1999). In descending order of predictability of geographical location and ecological stability, these are terrestrial (usually ice free), landfast ice (stable ice attached to land or prevented from moving by topographic features such as coastal islands and bays), and pack ice (ice floes size that continuously drift, break up, and raft together in response to wind and currents). Here, we are only concerned with pack ice and landfast ice and how they may influence the development of population structure of seals that live and reproduce in these habitats. The relatively unlimited availability and dynamic characteristics of pack ice, combined with aquatic mating and (predominantly) wide distribution of seals at low densities in breeding habitat, make fidelity of individuals to the same areas more difficult (or less necessary) and mating with the same groups of breeding animals in successive years less likely (Stirling 1975; Stirling 1983). These characteristics likely reduce the probability of population structure developing in species that breed on pack ice, even when they aggregate in large numbers in the same general areas, such as harp (*Pagophilus groenlandica*) or hooded (*Cystophora cristata*) seals. For example, the pack-ice-breeding hooded seal shows a lack of genetic structure for both microsatellite and mitochondrial DNA across its entire range from Atlantic Canada to east Greenland (Coltman *et al*. 2007). Similarly, harp seals of the Northwest Atlantic sampled from the Gulf of Saint Lawrence and off the coast of Newfoundland and Labrador were found to be genetically indistinguishable, as were harp seals from the Greenland Sea and White Sea of the Northeast Atlantic (Meisfjord & Sundt 1996; Perry *et al*. 2000). However, genetic differentiation between the northwest and northeast areas is considerable (Meisfjord *et al.* 1996; Perry *et al*. 2000).

Landfast ice is intermediate between the unpredictability of the constantly moving drifting pack and the absolute stability of terrestrial breeding sites. Mature adult Weddell and ringed seals overwinter in landfast ice where they must self-maintain their breathing holes, although where they are able to do so is significantly influenced by factors such as glacial movement, tidal action, and patterns of freeze-up. Males maintain underwater territories below the fast ice which allows them to restrict the subice mobility of potential competitors by blocking their access to breathing holes and thus may mate with more than one female (Stirling 1983; Gelatt *et al*. 2001; Harcourt *et al*. 2007).

In contrast with the ice-breeding phocids, the breeding habitat of species that mate on land (mainly islands) is completely predictable in its location and stability, resulting in natal fidelity for both males and females. Furthermore, the ability of dominant males breeding on land to limit access to reproductive females by competitors results in the development of sexual dimorphism and polygyny (Bartholomew 1970) which, in combination with fidelity to natal sites for reproduction, likely results in the development of population structure. Land-breeding pinnipeds that show significant population structure consistent with natal fidelity to predictable breeding habitat include harbour seals (*Phoca vitulina,* Stanley *et al*. 1996; Westlake & O'Corry-Crowe 2002) and southern elephant seals (*Mirounga leonine,* Hoelzel *et al*. 2001). Grey seals (*Halichoerus grypus*) breed on both land and ice. Land-breeding grey seals show evidence of genetic structure between colonies in Britain (Allen *et al*. 1995), and between the western North Atlantic, Baltic and Norwegian populations (Boskovic *et al*. 1996). However, in the western North Atlantic, the pack-ice-breeding population of the Gulf of Saint Lawrence is genetically indistinguishable from the land-breeding population of Sable Island (Boskovic *et al*. 1996). In comparison to the high degree of population structure demonstrated in some land-breeding species, we hypothesized that population structure would be lowest (or absent) in species that breed in pack ice and that population structure of those species breeding in landfast ice would be intermediate between those breeding on pack ice and land.

Several life-history parameters have been associated with the development of population structure (Stirling & Thomas 2003). In their possible descending order of importance, factors suggested to influence the development of population structure include natal philopatry, geographically variable vocal repertoires, female gregariousness, and the ability of dominant males to limit or reduce access to reproductive females (Table 1). Of the six species in this study, only the Weddell seal, which breeds on landfast ice, is known to possess all these characteristics. The only pack-ice phocid known to exhibit population structure, before this study, is the harp seal (*P. groenlandica*) which exhibits the first three characteristics. None of the remaining five species in this study is known to exhibit more than one of these characteristics and the degree of fidelity to natal sites for breeding is unknown for all but the Weddell seal. In the absence of additional information, we hypothesized that the presence of geographical variation in the repertoire of Ross, leopard, and bearded seals might be an indicator of the presence of population structure because it seemed unlikely that animals would exhibit a local repertoire unless they either remained resident in specific areas or at least returned to their natal areas for reproduction. Male ringed seals maintain their own breathing holes in the fast ice of the Arctic, as do Weddell seals in the Antarctic, which enables them to restrict the movements of other males and thus their access to resident adult females. Because of similarities in the ecology of Weddell and ringed seals, resident in the fast ice of Antarctica and the Arctic, respectively, we hypothesized that ringed seals might exhibit population structure. We therefore predicted that we would find significant population structure in all ice-breeding species with the exception of the crabeater seal, with more

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Table 1 Life-history characteristics of ice-breeding phocid seals in the Arctic and Antarctic in relation to breeding habitat. Species are ordered in their descending rank of genetic structure predicted by breeding habitat and life-history characteristics

Pupping and breeding habitat used by selected ice-breeding phocid seals		Life-history characteristics				Population structure θ (F_{ST})
		Fidelity to natal site for breeding	Geographically variable underwater vocalizations	Females gregarious when breeding	Males able to limit access to females	
Fast ice	Weddell seal	yes	yes	yes	yes	0.030*
	Ringed seal	unknown	no	no	yes	0.005*
Pack ice	Harp seal	yes	yes	yes	no	low‡
	Hooded seal	yes	unknown	yes	while on ice	0.000†
	Leopard seal	unknown	yes	no	no	0.001*
	Ross seal	unknown	yes	no	no	0.006*
	Bearded seal	unknown	yes	no	no	0.064*
	Crabeater seal	unknown	no	no	only while on ice	0.003*

*This study; †Coltman *et al*. (2007); ‡significant differences in allozyme allele frequency but not DNA fingerprint bandsharing reported by Meisfjord *et al.* (1996).

pronounced genetic differentiation in fast-ice-breeding species which have more predictable breeding habitat and likely natal fidelity. We tested these predictions by quantifying the population structure of six ice-breeding phocid seal species using microsatellites.

Materials and methods

Sample collections

To obtain material suitable for DNA extraction from the complete circumpolar distribution of each species, we used samples of fresh skin, muscle, blood, bone, or teeth collected during scientific research expeditions, from animals shot during exploratory sealing expeditions, or from animals harvested for sled dog food near Antarctic research stations. Samples of skin, blood, or teeth and were mostly collected from 1980 to the present. Preliminary analyses did not detect any temporal genetic differences within locations; therefore, we pooled samples collected in different years at the same location.

Three hundred and three crabeater seals were sampled as either single individuals or in small groups in the pack ice during research expeditions aboard icebreakers (Table 2; Fig. 1). Most samples were obtained from the eastern Ross Sea, Amundsen Sea and Bellingshausen Sea, from the west coast of the Antarctic Peninsula, and small numbers were also sampled from McMurdo Sound to the Southern Indian Ocean. A total of 150 leopard seal samples were obtained from six geographical regions including three sub-Antarctic islands (Heard, Macquarie, and Bird Island at South Georgia), the pack ice surrounding the South Orkney Islands, the west side of the Antarctic Peninsula, and in the Eastern Ross Sea–Amundsen Sea (Table 2). Ninety Ross seal samples were obtained from four geographical regions: the Ross Sea, the Queen Maud Land coast near the Norwegian Base Maudheim, the Queen Maud Land pack ice between South Africa and their Antarctic Expedition Base SANAE III, and the pack ice surrounding the South Orkney Islands. A total of 893 Weddell seals were sampled from 23 geographical areas including breeding colonies near research stations during the period of parturition and mating and later in both the landfast and pack ice after the end of breeding activity in early December. Breeding colonies were sampled near the Antarctic research stations of McMurdo, Davis, Syowa, Signy, and from Larsen Harbour, South Georgia, which remains ice free throughout the year. Non-breeding groups were also sampled in the dense pack ice of the Ross Sea and off the coast of Queen Maud Land (Fig. 1).

Of the arctic phocids, 119 bearded seal samples were collected from six geographical areas (Table 2, Fig. 1). Specimens were obtained from two regions in close proximity in the Bering Sea (Gulf of Anadyr and Saint Lawrence Island) during a joint USSR–USA cruise aboard the ZRS Zaslonovo. Samples from the Eastern Beaufort Sea were collected over almost two decades. Three areas were sampled in the Atlantic Ocean basin including the Newfoundland–Labrador coast (Canada), Qaanaaq (Greenland), and Svalbard (Norway). A total of 303 ringed seals were sampled from eight geographical locations, including western Alaska, Holman/Minto Inlet, Arviat, Iqualuit, Grise Fjord, Qaanaaq, Svalbard, and the White Sea (Table 2, Fig. 1).

Laboratory analysis

DNA was extracted using the QIAquick DNA extraction system (QIAGEN) from skin, muscle, blood, and bone and tooth drillings. Microsatellite analysis was performed using

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Table 2 Sampling location, two letter identifier, sample size, expected heterozygosity (H_E), F_{IS} (*$P < 0.05$, **$P < 0.01$) for six ice-breeding phocid seals

Sampling location	ID	N	Date	H_E	F_{IS}
(a) Crabeater seals					
Ross Sea	RS	254	1994–2000	0.85	0.004
Antarctic Peninsula	AP	37	1986–2000	0.85	0.059
McMurdo Sound to South Indian Ocean	SI	12	1993–1999	0.85	0.005
(b) Leopard seal					
Ross Sea	RS	13	1999–2000	0.72	0.028
Antarctic Peninsula	PN	32	1985–1988	0.72	–0.013
South Orkney Islands	SO	33	1964	0.73	0.061*
Bird Island, South Georgia	BI	57	1995–1996	0.74	0.000
Macquarie Island	MQ	7	1988	0.73	0.001
Heard Island	HD	8	1988	0.76	–0.039
(c) Ross seal					
Ross Sea	RS	42	1999–2000	0.74	–0.018
Queen Maud Land (Norwegian)	NA	20	2001	0.72	–0.042
Queen Maud Land (South African)	QM	16	1979–1988	0.70	0.081**
South Orkney Islands	SO	12	1964	0.72	0.008
(d) Weddell seal					
Queen Maud Land 1	Q1	9	2001	0.73	–0.011
Queen Maud Land 2	Q2	11	2001	0.74	–0.007
Syowa 1	S1	62	1999	0.73	–0.001
Syowa 2	S2	14	1999	0.76	0.055
Tryne Fjord	TF	34	1995–2000	0.73	0.003
McCallie Rocks	MR	25	1995–2000	0.75	–0.022
Long Fjord	LF	80	1995–2000	0.64	0.000
Cape Washington	CW	45	1997–1999	0.73	0.045*
Out North	ON	114	1997–1999	0.74	–0.007
Out South	OS	85	1997–1999	0.75	0.005
Scott Base	ST	30	1966	0.75	0.025**
Big Razorback Island	BR	96	1996	0.74	0.007
Close	CL	61	1997–1999	0.76	0.039
Lewis Bay	LB	15	1997–1999	0.74	0.064
White Island	WI	18	1991–2000	0.55	–0.179
Bay of Whales	BW	38	1999–2000	0.72	0.001
Cape Colbeck	CC	23	1999–2000	0.74	–0.006
Floe A	FA	32	1999–2000	0.74	0.005
Floe B	FB	17	1999–2000	0.78	–0.001
Floe C	FC	16	1999–2000	0.74	0.014
Siniff Bay	SB	29	1999–2000	0.74	0.034
Signy Island, South Orkney Islands	SO	26	1996	0.63	–0.058
Larson Harbor, South Georgia	SG	13	1998	0.66	–0.024
(e) Bearded seals					
Gulf of Anadyr, Russia	GA	25	1991	0.66	0.027
Saint Lawrence Island, USA	SL	28	1991	0.69	0.096
Beaufort Sea, Canada	BF	16	1973–1996	0.65	0.080
Labrador Sea, Canada	LD	16	1995–1999	0.61	0.013
Qaanaaq, Greenland	QA	16	1990s	0.62	0.063
Svalbard, Norway	SV	18	1990s	0.59	–0.109
(f) Ringed seal					
Alaska, USA	AK	23	1984	0.89	–0.006
Holman/Minto Inlet, NWT, Canada	MN	107	1994–1999	0.88	0.024*
Arviat, Nunavut, Canada	AV	28	1998	0.89	0.004
Iqaluit, Nunavut, Canada	IQ	29	1998	0.88	0.041*
Grise, Fjord, Nunavut, Canada	GF	31	1998	0.88	0.005
Qaanaaq, Greenland	QA	30	1998	0.88	–0.007
Svalbard, Norway	SV	30	1990s	0.88	0.011
White Sea, Russia	WS	25	1998	0.84	0.000

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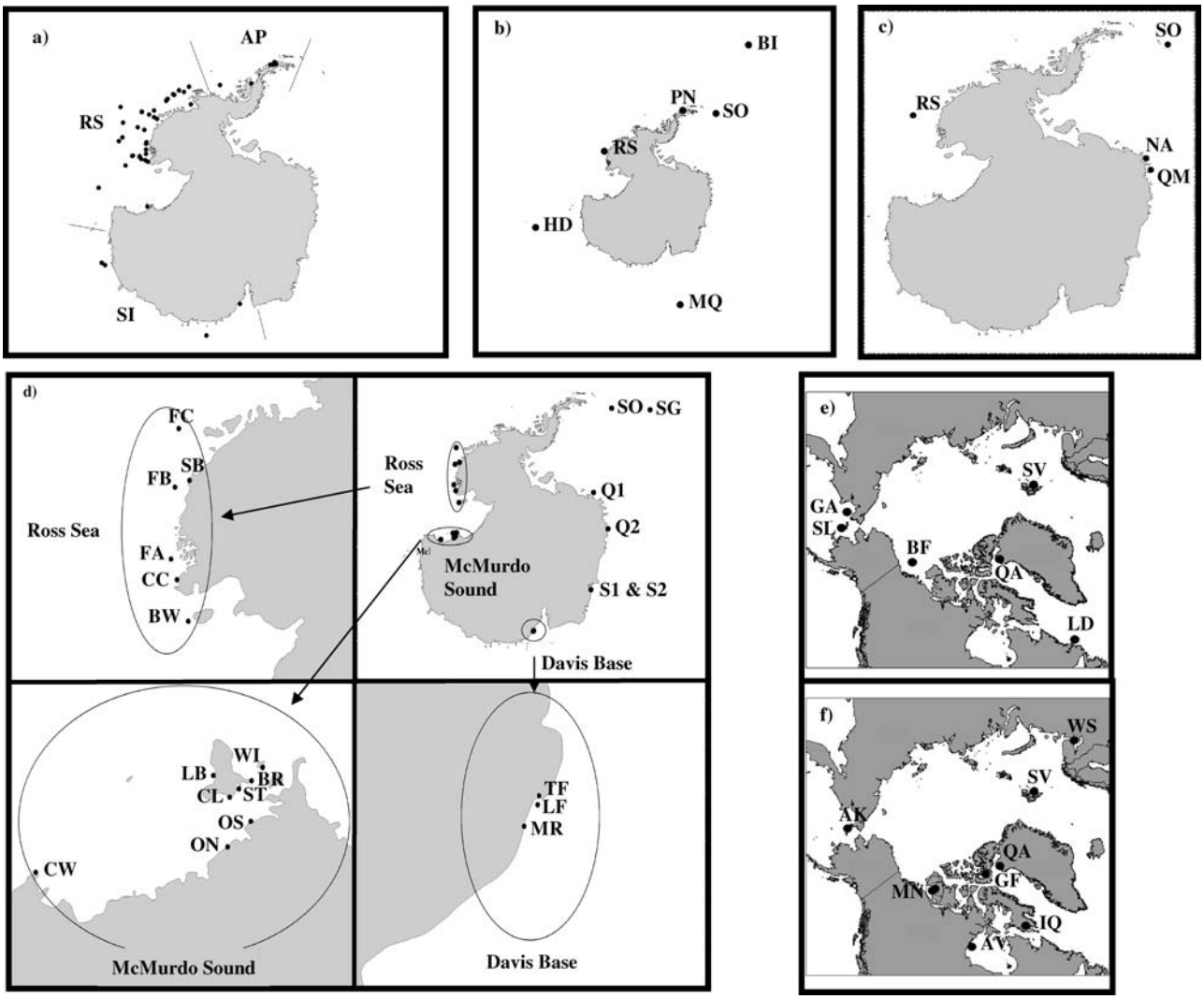

Fig. 1 Sampling locations for ice-breeding seals, for legend see Table 1. Points indicate individual locations for crabeater seals (a) and aggregate sample locations for leopard seals (b), Ross seals (c), Weddell seals (d), bearded seals (e), and ringed seals (f).

Applied Biosystems' fluorescence-based technology on either a 373-A or 377 automated DNA sequencers. The 24 microsatellite primer sets used for analysis were cloned from a variety of phocid species (Allen *et al*. 1995; Goodman 1997; Davis *et al*. 2002). One marker cloned from North American black bear (G1A) was also used (Paetkau & Strobeck 1994). Different subsets of loci for each species were selected based on their relative performance with low concentration DNA (from bone and teeth). A total of 15 loci were used in Weddell seal, 14 in leopard seal, 13 in the bearded seal, 11 in the ringed seal and 9 in each of the Ross seal and crabeater seal (Table 3). Two loci (Hl-8 and Hl-16) were used in all species. Polymerase chain reaction (PCR) conditions were identical to those used in a preliminary study of Antarctic seals (Davis *et al*. 2000) and a recent study of hooded seals (Coltman *et al*. 2007).

Statistical analysis

We first assessed levels of variation at each locus, tested for Hardy–Weinberg equilibrium (HWE), estimated *F*-statistics (Weir & Cockerham 1984) and genetic differentiation for each species overall using FSTAT 2.93 (Goudet 1995) and GENEPOP (Raymond & Rousset 1995) assuming geographically designated subpopulations. Confidence intervals for the variance components and tests for differentiation over all subpopulations were assessed by randomization in FSTAT (Goudet 1995). Pairwise *F*-statistics and exact tests for HWE and pairwise genetic differentiation between subpopulations were implemented in GENEPOP (Raymond *et al.* 1995). We assessed isolation-by-distance relationships using 2-way Mantel tests implemented in GENEPOP by comparing pairwise genetic distance (F_{ST}) to minimum

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Table 3 Polymorphism characteristics (H_E, expected heterozygosity; k, number of alleles) of microsatellite loci used to genotype polar phocid seals

	Crabeater seal (N = 303)		Leopard seal (N = 150)		Ross seal (N = 90)		Weddell seal (N = 893)		Bearded seal (N = 119)		Ringed seal (N = 303)	
Locus	H_E	k	H_E	k	H_E	k	H_E	k	H_E	k	H_E	k
G1A*	0.92	21	0.87	15	0.87	16	0.75	17	.	.	.	.
Hl-8*	0.91	24	0.87	14	0.82	14	0.87	16	0.83	15	0.91	23
Hl-14*	.	.	0.75	11	.	.	0.83	16	.	.	.	.
Hl-15*	.	.	0.81	13	0.62	6	0.60	23	.	.	0.94	35
Hl-16*	0.89	16	0.31	6	0.65	11	0.79	12	0.86	23	0.91	26
Hl-20*	.	.	0.85	14	0.85	13	0.77	14	0.79	8	.	.
Hg4.2†	.	.	.	.	.	.	.	.	0.75	11	0.93	32
Hg6.1†	.	.	.	.	.	.	.	.	0.79	12	0.92	27
Hg6.3†	.	.	.	.	.	.	.	.	0.70	8	0.88	16
Hg8.9†	.	.	.	.	.	.	.	.	0.80	9	.	.
Hg8.10†	.	.	.	.	.	.	.	.	0.52	3	0.73	23
Lc-6*	0.90	19	.	.	.	.	0.89	16	.	.	0.88	23
Lc-13*	.	.	0.88	11	.	.	.	.	.	.	.	.
Lc-18*	.	.	0.76	11	0.96	32	.	.	0.57	6	0.85	27
Lc-26*	0.81	14	.	.	.	.	0.84	14	.	.	.	.
Lc-28*	0.68	10	0.79	14	0.56	5	0.33	6	0.80	8	.	.
Lw-4*	0.94	50	0.87	23	.	.	0.83	25	.	.	.	.
Lw-7*	.	.	0.33	4	0.32	5	0.65	10	0.54	5	0.38	11
Lw-10*	0.69	12	0.93	21	0.91	20	0.88	16	.	.	.	.
Lw-11*	0.91	20	.	.	.	.	0.86	25	.	.	.	.
Lw-16*	.	.	0.67	9	.	.	0.79	12	.	.	.	.
Lw-20*	.	.	0.58	9	.	.	0.77	14	.	.	.	.
SGPV10‡	.	.	.	.	.	.	.	.	0.24	4	.	.
SGPV11‡	.	.	.	.	.	.	.	.	0.65	7	0.88	31
Total loci	9		14		9		15		13		11	

*Davis *et al*. 2002; †Allen *et al*. 1995; ‡Goodman 1997.

permanent ice-free sea distances calculated using ARCGIS. We used the Bayesian methodology of STRUCTURE (Pritchard *et al*. 2000) to determine the level of genetic substructure in the data set independently of sampling areas. We assumed an admixture model with correlated allele frequencies (Falush *et al*. 2003). To estimate the number of subpopulations (K), five independent runs of K = 1–10 were carried out at 500 000 Markov chain Monte Carlo (MCMC) repetitions following a burn-in of 100 000 repetitions for each species. The most probable number of subpopulations was identified using the criteria described in Evanno *et al*. (2005). The most probable number of subpopulations is therefore assigned to the value of K that shows the maximum increase in Ln[Pr($X \mid K$)] over successive increases in K.

Results

Microsatellite genotyping

Complete multilocus genotypes were obtained for 1815 of 1855 (97.8%) of the samples typed. Less than 1% of data was missing for each species. Of the 40 individuals that had missing data, 34 were not typed at a single locus and six were missing data for two loci. Missing data were evenly distributed over loci. Considerable diversity was observed in each species (Table 2; Table 3), and within species, no two samples had the same genotype.

Crabeater seals. No locus showed evidence for deviation from HWE in the crabeater seal sample at the population level after Bonferroni correction for multiple comparisons (eight loci, each $P > 0.0063$). Variance components for the geographically designated populations were not significantly different from zero (Table 4) with very little of the genetic variance partitioned between subpopulations ($\theta = 0.003$). There was a marginally significant difference in allele frequency among subpopulations overall ($P = 0.045$; Table 4). Pairwise comparisons showed little differentiation ($\theta < 0.01$) and no significant differences in allele frequency between subpopulations (Table 5). STRUCTURE analysis indicated that the most likely number of clusters was one ($K = 1$; Fig. 2).

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Table 4 Genetic structure of geographically designated ice-breeding seal populations quantified by *F*-statistics (Weir *et al.* 1984). *P* value (*P*) indicates the statistical significance of a permutation test for $\theta > 0$

Species	*N*	*F* (F_{IT})	θ (F_{ST})	*f* (F_{IS})	*P*
(a) crabeater seals	3	0.014 (–0.001, 0.029)	0.003 (–0.000, 0.007)	0.011 (–0.005, 0.027)	0.045
(b) leopard seal	6	0.012 (–0.010, 0.036)	0.001 (–0.002, 0.006)	0.011 (–0.010, 0.033)	0.001
(c) Ross seal	4	0.004 (–0.040, 0.038)	0.006 (0.000, 0.011)	–0.002 (–0.044, 0.033)	0.221
(d) Weddell seal	23	0.034 (0.026, 0.042)	0.030 (0.025, 0.035)	0.003 (–0.001, 0.010)	0.000
(e) bearded seals	6	0.098 (0.063, 0.140)	0.064 (0.046, 0.084)	0.036 (0.009, 0.068)	0.000
(f) ringed seal	8	0.019 (0.006, 0.031)	0.005 (0.003, 0.007)	0.013 (0.001, 0.025)	0.000

Leopard seals. No locus showed evidence for deviation from HWE in leopard seals after Bonferroni correction for multiple comparisons at the population level (14 loci, each $P > 0.0036$). Variance components for the geographically designated populations were not significantly different from zero (Table 4) with very little of the genetic variance partitioned between subpopulations ($\theta = 0.001$). There were statistically significant differences in allele frequency among subpopulations overall ($P = 0.001$; Table 4) largely attributable to differences involving the small Macquarie and Heard Island samples (Table 5). Genetic and geographical distances were weakly correlated ($r = 0.143$, $P = 0.27$; Fig. 3). STRUCTURE analysis indicated that the most likely number of populations was one ($K = 1$; Fig. 2).

Ross seals. No locus showed evidence for deviation from HWE in Ross seals after Bonferroni correction for multiple comparisons (nine loci, each $P > 0.0056$). Variance components for the geographically designated populations were not significantly different from zero (Table 4) with very little of the genetic variance partitioned between subpopulations ($\theta = 0.006$). There were no significant differences in allele frequency among subpopulations ($P = 0.221$; Table 4). Pairwise comparisons showed little differentiation (θ up to 0.0157) with only one nominally significant difference ($P < 0.05$) in allele frequencies between the Ross Sea and South African Queen Maud Land subpopulation samples (Table 5). Genetic and geographical distances were weakly correlated ($r = 0.33$, $P = 0.27$; Fig. 3). STRUCTURE analysis indicated that the most likely number of populations was one ($K = 1$; Fig. 2).

Weddell seals. One locus showed evidence for deviation from HWE in Weddell seals sample after Bonferroni correction for multiple comparisons at the population level (1 of 15 loci with $P < 0.0033$). All variance components for the geographically designated subpopulations were significantly different from zero (Table 4) with a measurable fraction of the genetic variance partitioned between subpopulations overall ($\theta = 0.030$). There were significant differences in allele frequency among subpopulations ($P < 0.001$; Table 4). Pairwise comparisons showed considerable differentiation between some subpopulations (θ up to 0.2118) and significant differences in allele frequency between most subpopulation pairs (Table 5). Genetic and geographical distances were weakly correlated ($r = 0.163$, $P = 0.03$; Fig. 3). STRUCTURE analysis indicated that the most likely number of clusters was three ($K = 3$; Fig. 2). Patterns of admixture indicated that one distinct cluster (cluster 1; Table 6) was highly represented (i.e. 81 individuals with $Q > 0.75$) among a subset of the individuals sampled in the Davis Base area. Most of these (78 of 80) were sampled in region called Long Fjord, a deep narrow fjord near the Davis Station in the Australian Antarctic region (Fig. 1). Three other individuals with $Q > 0.75$ were sampled from other areas within 20 km of Long Fjord: two from Tryne Fjord and one from the McCallie Rocks. A second cluster (cluster 2; Table 6) was highly represented (i.e. 38 individuals with $Q > 0.75$) in samples from South Georgia ($N = 13$ of 13 samples with $Q > 0.75$) and the South Orkney Islands ($N = 25$ of 26 samples with $Q > 0.75$). Cluster 3 was moderately prevalent in most other continental samples, and all of the remaining subpopulations showed a mixture of cluster 2 and cluster 3 genetic backgrounds.

Bearded seals. No loci showed evidence for significant deviation from HWE in bearded seals after Bonferroni correction for multiple comparisons at the population level (13 loci, each $P > 0.0038$). All variance components at the geographically designated population level were significantly different from zero (Table 4) with moderate genetic variance partitioned between subpopulations ($\theta = 0.064$). There were significant differences in allele frequency among subpopulations ($P < 0.001$; Table 4). Pairwise comparisons showed considerable differentiation between subpopulations (θ up to 0.123) and significant differences in allele frequency between most subpopulation pairs (Table 5) with the exception of comparisons between the two subpopulations sampled in the Bering Sea (Saint Lawrence Island and the Gulf of Anadyr) and between the Labrador Sea and Qaanaaq, Greenland. Genetic and geographical distances were positively correlated ($r = 0.46$, $P = 0.11$; Fig. 3). STRUCTURE analysis indicated that the most likely number of populations was two ($K = 2$; Fig. 3). The first cluster was

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comprised of animals sampled in the Bering Sea of the western Arctic from Saint Lawrence Island and the Gulf of Anadyr (Table 6). All animals sampled from these two populations had greater than 60% of genetic background attributed to this cluster (minimum $Q = 0.64$). One sample from the Beaufort also showed a high cluster 1 genetic background ($Q = 0.76$). All of the remaining samples from the eastern and high Arctic assigned to the second cluster.

Ringed seals. No locus showed evidence for deviation from HWE in ringed seals after Bonferroni correction for multiple comparisons (11 loci, each $P > 0.005$). Variance components for the geographically designated populations were significantly different from zero (Table 4) with very little genetic variance partitioned between subpopulations ($\theta = 0.005$). Allele frequencies differed significantly among subpopulations overall ($P < 0.001$; Table 4). Analysis of pairwise differences showed little differentiation between

Table 5 Pairwise fixation indices expressed as percentage of genetic variance ($\theta \times 100$; below diagonal) and tests for differentiation between geographically designated seal populations (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$)

Crabeater	RS	AP	SI
RS		—	—
AP	0.05		—
SI	0.22	0.04	

Leopard	RS	PN	SO	BI	MQ	HD
RS		—	—	—	**	**
PN	0.45		*	—	***	*
SO	0.09	0.41		—	***	—
BI	0.12	–0.06	–0.28		*	—
MQ	1.10	1.04	0.98	0.24		—
HD	2.08	0.47	–0.29	–0.08	–0.01	

Ross	RS	NA	QM	SO
RS		—	*	—
NA	–0.07		—	—
QM	1.05	0.56		—
SO	1.57	–0.36	0.09	

Bearded	GA	SL	BF	LD	QA	SV
GA		—	***	***	***	***
SL	–0.20		***	***	***	***
BF	8.39	7.47		***	***	***
LD	7.70	7.63	6.28		—	**
QA	6.90	6.43	3.00	1.33		***
SV	12.33	11.95	6.17	2.08	3.23	

Ringed	AK	MN	AV	IQ	GF	QA	SV	WS
AK		—	—	—	—	—	—	***
MN	0.26		—	—	—	—	—	***
AV	0.13	–0.02		—	—	—	—	***
IQ	0.49	0.00	–0.01		*	—	—	***
GF	0.31	0.13	0.19	0.34		—	*	***
QA	0.28	–0.04	0.01	0.20	–0.12		—	***
SV	0.50	0.02	0.00	0.00	0.41	–0.08		***
WS	3.06	2.41	3.06	2.47	1.80	2.10	2.70	

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Table 5 *Continued*

Weddell seals

	Q1	Q2	S1	S2	TF	MR	LF	CW	ON	OS	ST	BR	CL	LB	WI	BW	CC	FA	FB	FC	SB	SO	SG
Q1		—	—	—	*	—	***	*	**	*	*	*	*	—	***	***	—	—	—	—	*	***	***
Q2	–0.77		—	—	**	—	***	—	—	—	—	—	*	—	***	***	—	—	*	—	—	***	***
S1	0.19	1.09		—	***	**	***	***	***	***	***	***	***	***	***	***	***	**	***	—	***	***	***
S2	–0.29	–0.47	–0.11		***	*	***	**	**	**	—	**	****	—	***	***	*	—	—	—	***	***	***
TF	0.95	1.21	0.78	1.17		—	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
MR	0.73	0.83	0.66	0.67	0.12		***	**	***	**	*	***	***	—	***	***	**	**	**	—	***	***	***
LF	8.70	8.18	7.73	9.00	5.44	5.65		***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
CW	0.57	0.11	1.29	0.34	1.09	0.57	7.37		—	—	—	—	*	—	***	*	*	*	*	—	***	***	***
ON	0.84	0.79	1.28	0.32	1.54	0.45	7.35	0.07		—	—	—	—	*	***	***	*	—	**	—	**	***	***
OS	0.63	0.78	1.24	0.31	1.15	0.48	7.43	–0.01	–0.01		—	—	—	—	***	***	**	*	***	—	**	***	***
ST	1.34	1.04	1.06	–0.08	1.31	0.16	7.02	0.37	0.11	0.27		—	—	—	***	***	*	—	*	*	***	***	***
BR	0.73	0.36	1.06	0.06	1.12	0.43	7.10	0.08	–0.02	–0.02	0.16		—	*	***	***	*	*	—	*	***	***	***
CL	0.61	0.68	1.21	0.21	1.32	0.51	6.77	0.03	–0.07	0.07	–0.12	0.02		—	***	***	*	*	***	—	***	***	***
LB	1.24	1.28	2.03	0.23	1.28	0.76	7.03	0.07	0.61	–0.02	0.29	0.38	0.15		***	***	**	***	***	***	***	***	***
WI	14.59	9.43	11.36	11.05	13.44	12.13	16.67	10.20	10.52	10.66	10.95	10.05	10.07	12.18		***	***	***	***	***	***	***	***
BW	1.56	1.23	1.78	0.46	1.56	0.78	8.17	0.38	0.67	0.75	0.75	0.61	0.53	1.90	10.46		**	***	***	***	***	***	***
CC	0.33	0.79	1.10	0.21	1.36	0.39	6.71	0.01	0.15	0.38	–0.01	0.04	–0.07	1.15	11.91	0.76		—	—	—	—	***	***
FA	0.22	0.73	0.96	0.38	1.69	0.91	9.03	0.27	0.08	0.39	0.71	0.16	0.33	1.31	11.70	1.15	0.42		—	—	*	***	***
FB	1.35	1.47	1.27	–0.28	1.44	1.21	8.87	0.46	0.95	1.06	0.57	0.56	0.82	0.38	13.51	1.25	0.57	0.89		—	**	***	***
FC	–0.55	0.20	0.73	–0.32	0.84	0.35	8.01	–0.29	–0.33	–0.30	0.31	–0.28	–0.36	0.06	11.31	0.44	–0.10	–0.46	0.33		—	***	***
SB	0.93	0.06	1.46	0.40	2.13	1.15	9.01	0.56	0.51	0.87	1.01	0.64	0.82	1.63	12.11	1.32	0.55	0.52	1.25	0.13		***	***
SO	11.15	10.25	9.46	9.87	10.70	9.16	15.13	9.35	8.74	9.74	8.41	9.06	8.84	10.37	20.79	11.27	9.50	8.69	9.01	9.69	8.68		***
SG	12.03	9.96	10.05	10.19	10.06	8.71	13.26	9.96	9.69	9.74	8.60	9.35	9.36	8.87	21.18	11.42	10.25	9.75	9.63	9.96	9.75	4.54	

most subpopulations except for the White Sea sample which differed significantly from all other subpopulations in allele frequency and showed modest differentiation (pairwise θ ranging from 0.018 to 0.031; Table 5). Genetic and geographical distances were positively correlated ($r = 0.52$, $P = 0.04$; Fig. 3). However, the STRUCTURE analysis clearly indicated that the most likely number of clusters was one ($K = 1$; Fig. 3).

Discussion

In this study, we quantified the degree of population structure in six species of polar ice-breeding phocids and evaluated whether those results indicated a pattern in relation to the stability of the breeding habitat and other life-history characteristics (Table 1). Our predictions were only partly born out, as evidence for significant population structure was found for only one fast-ice- and one pack-ice-breeding species.

Fast-ice seals

Antarctic Weddell seals showed variable degrees of population structure. In contrast to Weddell seals, ringed seals breeding in similar habitat in the Arctic displayed little evidence for genetic differentiation.

Ringed seals. There was little evidence for genetic differentiation between ringed seals in any of the areas sampled across the Canadian Arctic except for comparisons to individuals sampled in the White Sea. This evidence contrasts with the idea that ringed seals are sedentary (McLaren 1958) and, although adults that establish breeding territories in regions of prime breeding habitat may have site fidelity (Smith & Hammill 1981), it indicates extensive gene flow among regions. The exclusion of immature and young breeding animals from breeding habitat in the landfast ice suggests the possibility that this type of habitat may be limited, at least in some areas. If areas of consolidated annual ice with good snow cover (Smith 1987) in fjords and landfast ice between islands and coastlines (McLaren 1958) are indeed the preferred breeding habitat of ringed seals, then younger animals, which are excluded from these areas, must use less preferred habitat for breeding and may move in search of alernative habitat. However, most research on ringed seal pupping and breeding has been carried out in the fast ice, and the potential for extensive breeding in other areas, including pack ice, has not been quantitatively

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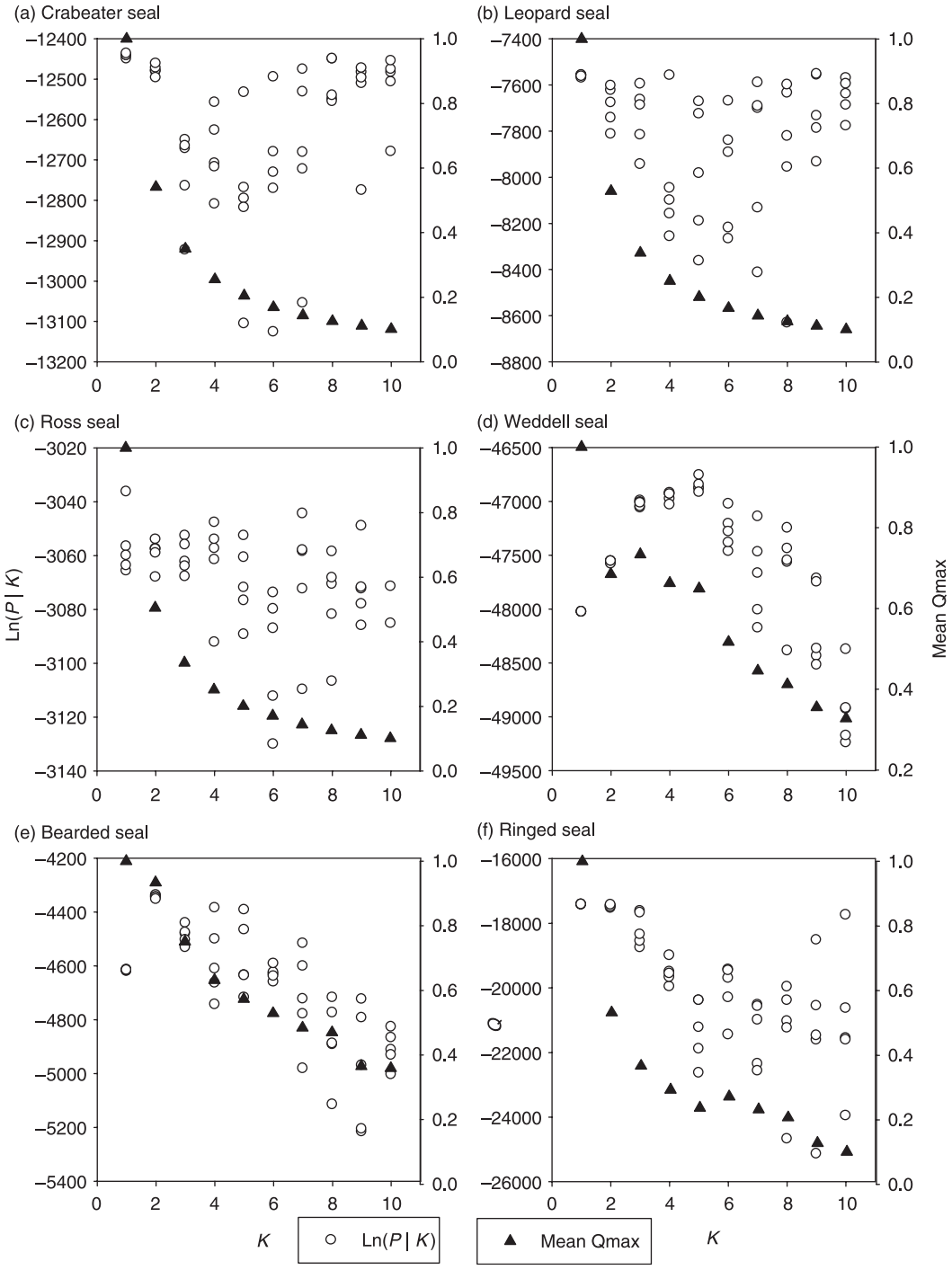

Fig. 2 Likelihood {Ln[Pr(*X* | *K*)]} and average cluster membership (mean maximum *Q* or proportion of ancestry for each individual assigned to a cluster) plots for STRUCTURE analysis of crabeater (a), leopard (b), Weddell (c), Ross (d), bearded (e), and ringed seals (f) using five runs at each *K* from 1 to 10. Geographical distances are the shortest sea surface distance between sample locations. Ln[Pr(*X* | *K*)] is the logarithm of the posterior probability (P_r) of the data (*X*) for a given number of clusters (*K*).

explored (Reeves 1997). Some evidence suggests ringed seals also breed in heavy pack-ice regions (Finley *et al*. 1983; Wiig *et al*. 1999) which may indicate they are more generalist in their habitat preference than has traditionally been thought. Like crabeater seals, young ringed seals also sometimes travel in large groups (Harwood & Stirling 1992) and several telemetry studies have now demonstrated that young seals travel substantial distances (Smith 1987;

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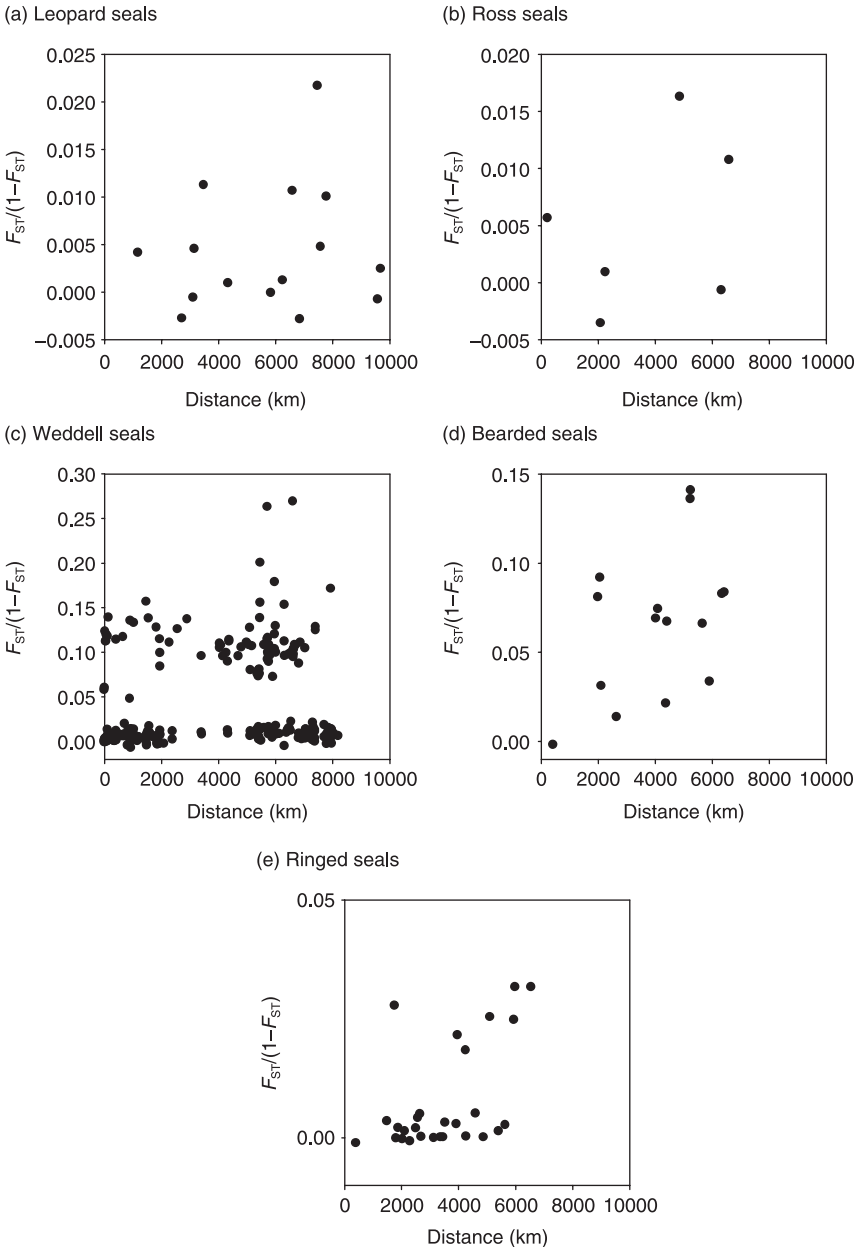

Fig. 3 Isolation-by-distance relationships for leopard (a), Ross (b), Weddell (c), bearded (d), and ringed seals (e). Geographical distances are the shortest sea surface distance between sample locations.

Kapel *et al*. 1998; Teilmann *et al*. 1999). It is not known if young animals return to their natal areas to breed or if they settle elsewhere and then, as adults, maintain fidelity to breeding areas. However, the lack of population structure suggests they do not return to natal areas to breed or, if some proportion does, they do not concentrate enough to overcome genetic dilution resulting from mixing with animals from adjacent areas. Therefore, even if older breeding individuals may show site fidelity, it appears that younger animals can move extensively throughout regions and settle away from their natal area, resulting in high levels of gene flow and limited genetic differentiation between regions.

Weddell seals. Weddell seal breeding colonies are distributed along the coastline of Antarctica in areas where tidal action, glacial movement, or other factors help to maintain cracks in the ice through winter where seals can breathe. Thus, from freeze-up in the fall through breakup (post-breeding) in the spring, movement of seals away from colonies is restricted. Although seals may be found in the offshore pack ice during summer, especially pups and nonbreeding individuals, adults overwinter in their natal colonies or nearby and return in early spring in time to breed. Although some of the populations used in this study were sampled from the same general areas used for previous allozyme studies, we sampled multiple breeding colonies within

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Table 6 Proportion of ancestry (*Q*) inferred for bearded and Weddell seal population clusters identified by a STRUCTURE analysis. The number in parentheses indicates the number of individuals sampled in each area that showed ancestry > 0.75 to that cluster

	Mean cluster membership (*Q*)		
Species and geographical subpopulation (*N*)	1	2	
Bearded seal			
Gulf of Anadyr, Russia (25)	0.94 (23)	0.06 (0)	
Saint Lawrence Island, USA (28)	0.95 (26)	0.05 (0)	
Beaufort Sea, Canada (16)	0.21 (1)	0.79 (10)	
Labrador Sea, Canada (16)	0.04 (0)	0.96 (16)	
Qaanaaq, Greenland (16)	0.07 (0)	0.93 (15)	
Svalbard, Norway (18)	0.02 (0)	0.98 (18)	
	1	2	3
Weddell seal			
Queen Maud Land 1 (9)	0.032 (0)	0.447 (2)	0.521 (3)
Queen Maud Land 2 (11)	0.044 (0)	0.375 (0)	0.581 (3)
Syowa 1 (62)	0.038 (0)	0.417 (8)	0.544 (16)
Syowa 2 (14)	0.019 (0)	0.358 (2)	0.623 (7)
Tryne Fjord (34)	0.186 (2)	0.449 (6)	0.365 (3)
McCallie Rocks (25)	0.093 (1)	0.483 (4)	0.424 (3)
Long Fjord (80)	0.948 (78)	0.026 (0)	0.025 (0)
Cape Washington (45)	0.058 (0)	0.438 (4)	0.504 (7)
Out North (114)	0.031 (0)	0.42 (17)	0.549 (30)
Out South (85)	0.032 (0)	0.408 (8)	0.560 (19)
Scott Base (30)	0.043 (0)	0.421 (4)	0.535 (6)
Big Razorback Island (96)	0.035 (0)	0.385 (10)	0.580 (32)
Close (61)	0.044 (0)	0.438 (5)	0.517 (9)
Lewis Bay (15)	0.056 (0)	0.416 (3)	0.528 (4)
White Island (18)	0.032 (0)	0.077 (0)	0.892 (16)
Bay of Whales (38)	0.029 (0)	0.357 (3)	0.614 (15)
Cape Colbeck (23)	0.061 (0)	0.413 (3)	0.526 (8)
Floe A (32)	0.016 (0)	0.482 (7)	0.502 (5)
Floe B (17)	0.017 (0)	0.489 (4)	0.493 (5)
Floe C (16)	0.017 (0)	0.423 (2)	0.560 (5)
Siniff Bay (29)	0.035 (0)	0.521 (6)	0.443 (4)
Signy Island, South Orkney (26)	0.037 (0)	0.927 (25)	0.035 (0)
Larson Harbor, South Georgia (13)	0.071 (0)	0.904 (13)	0.025 (0)

each region, allowing for an assessment of minimum distances over which population differentiation might occur. Significant genetic differentiation was found at a minimum geographical distance of approximately 700 km (for example, between McMurdo Sound and the Bay of Whales). Differentiation of Weddell seal populations, using analysis of vocal repertoires has been found at similar distances in studies examining differences in underwater vocalizations at macrogeographical (approximately 5000 km), and mesogeographical (600–2000 km) scales (Thomas & Stirling 1983; Thomas *et al*. 1988; Abgrall *et al*. 2003). No significant population structure was found at smaller distances, suggesting that dispersal over relatively short distances (less than 700 km) results in enough gene flow to effectively homogenize populations.

Genetic distance between breeding colonies was significantly correlated to physical distance supporting the contention that recruitment of an individual to a colony, other than place of birth, is limited by dispersal range. Juvenile dispersal is the most likely method of gene flow. Young Weddell seals appear to spend most of their time foraging in the pack ice (Stewart *et al*. 2003), where mixing of individuals born at different coastal breeding colonies occurs. Samples of Weddell seals collected in the offshore pack ice in summer (e.g. floes A, B and C) show little differentiation which also indicates that when these seals mature, most return to their natal site to breed.

The high degree of differentiation and apparent isolation of Weddell seal colonies on islands to the north of the species range was not unexpected and suggests that long-distance movements are rare. Isolation of these populations was expected not only because they are isolated by long distances but also because large expanses of unsuitable habitat exist between them and coastal breeding colonies. The small land breeding colony at Larsen Harbour, South Georgia, may be maintained by low levels of immigration

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from Signy Island (Croxall & Hiby 1983), as evidenced by the similar levels of admixture between these two locations (Table 6).

Weddell seals can also become physically isolated in the southern extremes of their range. Stirling (1972) identified a small apparently isolated colony of Weddell seals breeding at White Island, separated from nearby colonies in McMurdo Sound, by 20 km of ice shelf. No exchange of tagged seals has ever been observed between White Island and breeding colonies in southeastern McMurdo Sound, suggesting that the colony is completely isolated. Genetic studies have shown that the colony was founded within the last 100 years by fewer than 10 individuals (Gelatt 2001), and results here indicate lower levels of genetic variation than other Weddell seals populations (Table 2) and distinct genetic differentiation (Table 5, Table 6). High pup mortality and reduced reproductive rate may indicate inbreeding depression in this population. The founders of this population may have gained access to White Island following a brief break in the McMurdo ice shelf between 1947 and 1956, and were subsequently isolated. In the southern extremes of their range, Weddell seals may also become isolated due to infrequent geological events. At least two other similar colonies of Weddell seals, isolated by ice sheets have been reported. One apparently persists in the Bunger Hills (H. Burton, personal communication), and another of 200–300 seals was observed several times between 1957 and 1963 in rifts in the Ross Ice Shelf near Roosevelt Island to the south of the Bay of Whales (P. Smith, personal communication), suggesting that this mode of isolation may occur periodically. However, in a survey of the rifts near Roosevelt Island in January 2000, no seals or signs of seals were observed indicating that some of these isolated populations may not persist.

The high degree of differentiation of the breeding colony of Weddell seals in Long Fjord, near Davis station in the Australian Antarctic region, was not anticipated (Table 5, Table 6). There is no evidence that this colony was ever physically isolated, and it is unlikely that seals persisted in the Fjord during the last glacial maximum (Hodgson *et al*. 2001). Even if seals were isolated over geological timescales, seals now freely leave the Fjord and apparently few, if any, overwinter there (H. Burton, personal communication). However, some level of isolation has been maintained at least until recently, as samples of individuals over that time period are strongly differentiated from the nearby colonies (approximately 10 km) in Tryne Fjord and at McCallie Rocks. Of 80 seals sampled over this time in Long Fjord, only two individuals possessed genotypes that would suggest that they were immigrants with admixed backgrounds (Table 6). There is no clear explanation for this level of differentiation. Long Fjord is 25 km long and only 5 km wide, and is restricted by a narrow and shallow entrance. One possibility is that the physical characteristics of Long Fjord may accentuate a highly developed tendency towards local natal philopatry.

Pack-ice-breeding seals

No population structure was found in any of the three Antarctic pack-ice species (Ross, crabeater and leopard seal). This suggests high rates of gene flow among geographically distant subpopulations in all three species, including several sub-Antarctic islands. Each of these species therefore comprises a single panmictic genetic population distributed through the pack ice surrounding Antarctica. In contrast, we found some significant genetic differentiation in the bearded seal. The two subpopulations sampled in the Bering Sea (Saint Lawrence Island and the Gulf of Anadyr) appear to be genetically differentiated from the remaining subpopulations (Table 6).

Crabeater seals. We correctly hypothesized little genetic structure in crabeater seals. Previous molecular examinations of differentiation in crabeater seals using allozymes (Seal *et al*. 1971; Hofman 1975) and random amplified polymorphic DNAs (RAPD, Gelatt *et al*. 1995) have not found population structure. Crabeater seals have only one vocalization, compared to several in the other pack-ice species, and there is no evidence of geographical variation in their call. The use of floating pack ice for breeding and extensive movement by individual seals (halfway around the entire continent in 6 months for one individual; J. Bengston, personal communication) likely contributes to high levels of gene flow between regions around Antarctica.

Leopard seals. Of the three Antarctic pack-ice species, we hypothesized that leopard seals might be the most likely to exhibit population structure. Significant variation in the underwater vocalizations has been found between geographically distant locations at Palmer Peninsula and McMurdo Sound (Thomas & Golladay 1995). Also, known individual leopard seals have returned to hunt fur seal pups in the winter at two different sites in the sub-Antarctic islands in subsequent years (Walker *et al*. 1998; Hiruki *et al*. 1999) indicating that at least some animals in the population show a seasonal fidelity to specific areas and are not simply moving at random. However, seals sampled from six geographical locations in the pack ice and at sub-Antarctic islands displayed no genetic differentiation. It is possible that there is sufficient fidelity to foraging areas to reinforce the development of local geographical dialects that aid in cooperative hunting, however, there is sufficient gene flow to prevent the development of population structure.

Ross seals. Similar to leopard seals, despite evidence for geographical variation in their vocalizations, no evidence for population structure was found in Ross seals, a species

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that pups and molts in areas of dense pack ice but spends most of the rest of the year feeding alone in the open water north of the ice pack. High rates of gene flow were indicated among geographically distant populations in the Ross Sea and in the pack ice off Queen Maud Land. Although recent tracking of a limited number of Ross seals using satellite telemetry suggests that individuals return to the same areas of the pack ice in the year following tagging (Blix & Nordoy 1998), it is possible that over the lifetime of a seal fidelity to a particular region of pack ice is lost. Also, since Ross seals are distributed at such low densities the concentrations of females with geographical fidelity is not sufficient to facilitate the development of population structure. Fidelity to specific sites for breeding and molting would be difficult to maintain because of the high degree of annual variability in the distribution of ice generally and that it is constantly moving in response to wind and currents. The result is genetic homogenization of individuals throughout the range of Ross seals, and a single panmictic population. The closely related southern elephant seal offers an interesting comparison in ecological partitioning and the genetic consequences of mating on land or in pack ice. Both species make long foraging trips to the open sea, returning to breeding grounds only to mate and moult. Southern elephant seals return to highly predictable, spatially limited sub-Antarctic islands to the north of the feeding areas to breed, and consequently display marked population structure (Slade *et al*. 1998; Hoelzel *et al*. 2001). In contrast, Ross seals return to unpredictable, unlimited pack ice for breeding at very low densities, to the south of the feeding areas, and display no population structure.

Bearded seals. Bearded seals occupy two types of pack-ice habitat: the first type includes the polynyas and shorelead systems that parallel the mainland coast around the circumpolar basin (Stirling 1997). From freeze-up in the fall to breakup in the spring, the multiyear polar pack from the polar basin moves south and joins with the annual ice that forms along the coast. Cracks open and close along this system through the winter in response to winds and currents, but in general, movement along them is restricted and the greatest concentrations of bearded seals are in or near polynya areas. Thus, once freeze-up occurs in winter, the ability of bearded seals to move away from their overwintering sites is greatly reduced; a similar situation to Weddell seals in winter. Also like Weddell seals, in some of these coastal locations where the ice freezes up tightly, bearded seals sometimes have to self-maintain some of their own breathing holes, although usually for much shorter periods of time. It is interesting to note that the microsatellite analyses suggest separation distances of about 500–1000 km are enough for population structure to develop in both Weddell and bearded seals in areas where their movements are restricted by ice. The second type of pack-ice habitat occupied by bearded seals is that along the southern boundaries of the polar pack, such as in Davis Strait or the Bering Sea. Although the ice cover can be continuous, the ice is less consolidated and the seals have a greater ability to move during winter than those in the more tightly frozen shorelead systems that parallel the land masses. These differences in habitat, as well as geographical proximity, probably contribute significantly to the lack of differentiation between the two populations sampled in the Bering Sea (Saint Lawrence Island and the Gulf of Anadyr) as well as the evidence for limited gene flow among populations sampled in the Atlantic Ocean basin (Table 6).

Another common behavioural characteristic of Weddell and bearded seals that allow for the development of population structure is the presence of significant geographical variation in vocal repertoires (Thomas *et al.* 1983; Thomas *et al*. 1988; Cleator *et al*. 1989; Risch *et al*. 2007). In some cases, bearded seal dialects may vary significantly over distances of less than 250 km when polynya areas are separated by solid landfast ice with few cracks during late winter. Although there are apparently no restrictions to the movements or dispersal of bearded seals during summer or fall, they may show strong fidelity to natal sites similar to Weddell seals for their high degree of population structure to develop, however this has not yet been demonstrated.

Breeding habitat stability and ecological factors in relation to population structure

In general, there is a consistent pattern between breeding on stable terrestrial habitat and the development of population structure. Thus, we predicted that population structure in ice-breeding phocids would be more developed in species that breed in fast ice than in the less stable pack ice. However, our results did not support this prediction. While none of the Antarctic pack-ice species showed population structure, the bearded seal of the Arctic pack ice showed strong differentiation. Again in contrast, the fast-ice-breeding Weddell seal of the Antarctic showed clear population structure while the ringed seal, breeding in similar habitat in the Arctic, did not. These results suggest that the development of population structure in ice-breeding phocids is more complex than might be inferred simply on the basis of adaptation to their natal habitat. Thus, it is relevant to examine broader aspects of the evolution of population structure in the species that do or do not exhibit population structure in their respective polar regions.

In Table 1, we summarized life-history characteristics of the six ice-breeding phocids in this study that we hypothesized could be important to the development of population structure, or indicative of the existence of population structure, in what we speculated might be their

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order of relative importance. It seems obvious that population structure cannot develop unless there is fidelity to the natal area for breeding as adults; yet, this can only be confirmed in one species, the Weddell seal. The limitations on movement between breeding areas in winter and during the spring breeding season are similar in Weddell and bearded seals, and that those two species were the only ones to exhibit strong population structure also suggests that bearded seals have fidelity to their natal areas for breeding.

Both bearded seals and Weddell seals have well-documented geographical variation in their vocalizations as well as population structure. However, Ross seals and especially leopard seals, which have highly developed and geographically variable underwater vocal repertoires, did not exhibit population structure. It is not known if either species maintains fidelity to natal areas for reproduction, although some young leopard seals have been shown to have seasonal fidelity to winter feeding areas away from the pack ice. In comparison to harp seals, which undergo extensive movements but aggregate in large numbers at relatively high densities in widely separated natal areas to mate, Ross and leopard seals are both distributed throughout the Antarctic pack ice at low densities which is likely to confound the development of population structure even if individuals return to natal areas. However, the presence of geographically variable dialects suggests that adults may maintain sufficient fidelity to breeding areas to maintain dialects through learning but without enough separation between areas to develop population structure.

The two most numerically abundant species, crabeater and ringed seals, exhibit no population structure and high levels of diversity despite the preference of crabeater seals for pack ice and ringed seals for fast ice. Movement in the fast ice during winter is likely restricted and ringed seal males can probably restrict the access of competing males to breeding females. Although all the pack-ice phocids are vulnerable to predation to some degree, the pressure of predation on crabeater and ringed seals by leopard seals and polar bears is much higher than on any other pinniped (Siniff & Bengtson 1977; Siniff *et al*. 1979; Stirling & Øritsland 1995). Neither species appears to have any geographical variation in vocal repertoire. Furthermore, crabeaters give only one short, low-frequency monotonic call that would be more difficult to locate than a longer high-frequency vocalization. Ringed seals have only a small number of very short calls that are given with such low intensity that they are difficult to detect even at close range with a preamplifier on a hydrophone. Both of these adaptations are likely intended to reduce the ease of being located by a predator. Similarly, like ringed seals, young crabeater seals appear to aggregate in groups that may number in the low hundreds (Siniff *et al*. 1979; Harwood *et al.* 1992) and move through pack-ice areas but do not exhibit seasonal fidelity to particular areas so far as is known. This behaviour also likely functions to reduce the threat to individuals in the event a group is located by a predator. Conversely, breeding adults are widely distributed at low densities, whether in pack or landfast ice which may increase the risk of predation to individuals or their young. However, at low densities, increased search time on the part of predators may mean the majority of seals will not be located when they are most vulnerable. In comparison, harp and hooded seals aggregate on the pack ice to pup in very large numbers in the same general areas, although the specific location of the patches may vary between years. However, the pups are weaned and independent in only 10 days and the pack-ice areas used are near the floe edge where they are more vulnerable to breakup than is the breeding habitat of either crabeater or ringed seals. Thus, even if polar bears do locate the breeding patches, the risk of predation to an individual is low and the period of vulnerability sufficiently short that it does not break down the population structure that has evolved because of fidelity to breeding sites for reproduction.

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This work comprises part of Corey Davis' PhD thesis project work supervised by Curtis Strobeck who is now a Professor Emeritus at the University of Alberta. Corey is now a molecular biology technician in the Department of Biological Sciences at the University of Alberta with interests in molecular ecology and systematics. Ian Stirling is a marine mammal ecologist with particular interests in predator-prey relationships and the evolution of behaviour in ice-breeding seals. Dave Coltman induced this story to parturition following delayed implantation and a long period of gestation.

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